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Abandon all species concepts? A response

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In their attempted deconstruction of species concepts and of our recent reviews of the vertebrate literature on mitochondrial (mt) DNA variation, Hendry et al. (2000) champion two major theses. First, they contend that "mtDNA discontinuities do not closely match recognized taxonomic species" and, hence, that these molecular data help negate the notion that "species" (genetic discontinuities) exist in the natural world. Second, Hendry and coauthors advocate "abandoning the concept of species" (biological, phylogenetic, or otherwise), and adopting instead a new descriptive scheme that would group organisms at any level strictly by "specifying the amount of difference in various traits."

Both of these conclusions are couched in the authors' premise that adherence to traditional species' paradigms has blinded most biologists (ourselves included) to Hendry et al.'s (2000) view: that the species level of biological organization is no less arbitrary in concept or in practice than that for genus, order, or any other taxonomic level in a hierarchical classification. This is an old and recurring issue (Darwin 1859; Dobzhansky 1937; Mayr 1963). Without wishing to appear unduly stodgy in defense of more traditional species views (we too have serious reservations about conventional paradigms for biological classification; Avise and Johns 1999), we nonetheless take a rather different slant on these two main points.

First, with regard to the level of agreement between vertebrate taxonomic species and mtDNA phylogenetic discontinuities, the opposing judgments by us and by Hendry and colleagues merely reflect, we think, the difference between "viewing the taxonomic cup as mostly full versus partly empty". From our cited reviews of the available mtDNA literature on vertebrates, the uncontested facts are as follows: (a) *at least* 75% of suspected sister species (named taxa thought to be one another's closest living relatives) display pronounced mtDNA differences (this is why blatant exceptions such as the cichlid fishes in Lake Victoria attract such interest); (b) in nearly 50% of the taxonomic species surveyed, geographic populations have shown no major discontinuities in mtDNA phylogeny (Hendry et al. (2000) are mistaken when they write that these species were disregarded in the Avise and Walker (1999) review – to the contrary, they constitute the "one phylogroup per species" category in Figure 2 and in all data summaries); (c) in the remaining taxonomic species displaying salient mtDNA discontinuities, the number of "intraspecific phylogroups" thus far detected is small, typically only two to six; and (d) these pronounced phylogroups nearly always are allopatric [an important point almost totally neglected by Hendry et al. (2000)].

After taking into account several opposing biases (several of which Hendry and co-authors reiterate) in the existing data sets, we interpreted these collective observations as indicative of a surprisingly good level of agreement ("certainly within an order-of-magnitude") between the number of recognized taxonomic species of vertebrates and the number of salient discontinuities in mtDNA phylogeny (Avise and Walker 1999). This sentiment would hold true even if *all* of the known "intraspecific phylogroups" were to be elevated to "full-species" status. As emphasized repeatedly in our writings (e.g., Avise 1989, 2000), this is not to say that all current species-level taxonomic assignments are "correct" by molecular standards. But the current molecular data do suggest that when all the results are in, the final tally of salient genetic discontinuities in nature probably will not depart greatly from the number of taxonomic species

currently recognized by vertebrate systematists. This conclusion clearly carries importance for biodiversity analyses and conservation efforts (Reaka-Kudla et al. 1997).

From years of hands-on experience, we never cease to be impressed that even closely related vertebrate taxonomic species usually "stand out from one another like sore thumbs" in molecular genetic assays, whereas individuals within each phylogroup or species normally show remarkably tight connections (recent coalescence) in matrilineal history. Among other ramifications, such genetic findings have made it routinely possible for molecular ecologists to employ mtDNA and other molecular markers in detailed genetic analyses of hybrid zones (e.g. Avise and Saunders 1984; Lamb and Avise 1986; Hewitt 1988; Scribner and Avise 1994; Avise et al. 1997) and to assist in diagnosing otherwise cryptic sibling species (e.g. Avise and Zink 1988; Knowlton 1993) (reviews in Avise 1994).

As elaborated extensively by Avise (2000), these matrilineal unities within and discontinuities between biological entities probably register historical demographic factors primarily. For example, unexpectedly small evolutionary effective population sizes for many taxonomic species and intraspecific phylogroups (Avise et al. 1988) appear to have tightened genealogical connections within such units by fostering relatively recent coalescent events, whereas frequent lineage and population extinctions often may have sharpened the boundaries between them. In our view, such insights about the historical, nonequilibrium dynamics of population demography, and their ineluctable consequences in promoting unities and discontinuities in micro-genealogy, have been among the most important of the broader empirical and conceptual contributions of the field of molecular phylogeography (Avise 2000).

Our literature reviews were designed expressly to address the topics of "species" and "speciation" in sexually reproducing organisms from an unorthodox vantage point – provided by an asexually transmitted molecule. By virtue of predominant maternal inheritance, mtDNA haplotypes are connected to one another primarily via vertical pathways through extended organismal pedigrees, rather than "horizontal" ties *per se* of interbreeding between males and females. This is precisely why it is especially intriguing, in our view, to find a reasonably good agreement between the number of current taxonomic species (most of which were identified in the philosophical era of biological species concepts) and the number of phylogenetic clusters registered as distinctive branches in mtDNA gene trees. We interpret such agreement as evidence for our contention that biological species concepts and *properly formulated* versions of a phylogenetic species concept often will tend to converge, in principle and practice, on a recognition of the more salient of recent biological discontinuities in the natural world (Avise and Ball 1990; Avise and Wollenberg 1997).

We are acutely aware of many cases (sometimes involving taxa of special conservation interest; e.g. Laerm et al. 1982; Avise 1989; Avise and Hamrick 1996) where, in their species' descriptions, taxonomists seem to have "gotten it wrong" by the standards of molecular evidence. Indeed, if this were not the case, there would be little incentive for molecular reevaluations. Hendry et al. (2000) are not incorrect to focus on such disagreements between mtDNA boundaries and taxonomic species; such emphasis is a matter of taste. Nonetheless, we remain impressed by how often traditional vertebrate systematists would appear to have gotten things principally right.

Hendry et al. (2000) correctly emphasize that there is considerable overlap in the frequency distributions of mtDNA genetic distance between intraspecific phylogroups and sister species. Because of the many known geographic, temporal, and demographic variables associated with different biological speciations, and because of the great heterogeneity in taxonomic standards applied by different organismal specialists, we would be astounded if this were not the case. Furthermore, biological speciation in most cases is a temporally extended phenomenon rather than a point event in time. From mtDNA evidence, we estimated that vertebrate speciations require on average two million years or more to go to completion, although there is a huge variance about this mean (Avise et al. 1998; Avise and Walker 1998). This implies that historical separations of genealogical lineages ancestral to many of today's sister species and other congeners probably were initiated prior to the Pleistocene (Klicka and Zink 1997).

If biological speciation in vertebrates normally occurs over such an extended timeframe, then many gray areas must exist along the temporal continuum of black (conspecific status) to white (species status). Almost inevitably, these will generate taxonomic difficulties in any dichotomous scheme (such as that employing Latin binomials) that can only recognize populations as conspecific or not. But in our opinion, this is insufficient rationale to abandon all current

species *concepts*, for at least two reasons. First, even a strictly gradual and cumulative process of genetic divergence in the stream of heredity can and apparently does eventuate over evolutionary time in biological discontinuities (phylogroups and species) in nature, much as discrete drops of water from a leaky faucet can emerge from a continuous trickle within. Second, to cleanse from evolutionary thought all reference to species-formational processes (the emergence of reproductive isolation, and/or of phylogenetic separations) would be to leave a hopelessly sterile epistemological foundation for interpreting the origin and maintenance of biotic discontinuities in nature (Avise 2000).

This leads us to comment briefly on Hendry et al.'s (2000) second major thesis – that after firmly abandoning all species' concepts, a new scheme for biological organization should be adopted that recognizes taxa at any level strictly on some quantitative basis of how much they differ from one another in genetics, morphology, or other features. We are highly sympathetic to the general idea that far greater standardization is needed in taxonomic assignments, such that the field of systematics someday may move to a truly universal classification scheme that would convey far more useful comparative information than the non-standardized classifications currently in place (Avise and Johns 1999). In our view, this standardized system ideally would apply uniform or normalized ranking criteria to all organismal groups *above the level of species* such that, for example, a taxonomic genus, family, or tribe of whales would be equivalent in a scientifically informative sense to its taxonomic counterpart in birds, fruit flies, or any other organismal clade.

Indeed, we recently advanced and detailed an explicit proposal for one such standardized scheme, involving the concept of "temporal banding" (Avise and Johns 1999). For taxonomic ranks above the level of species, our basic idea is that absolute *evolutionary times* (e.g., geological ages) of phylogenetic separation (rather than any second-order correlates such as magnitudes of genetic or morphological divergence as in Hendry's et al. view) should in principle be the ultimate common denominator for universally ranking all forms of life. However, we do not recommend extending any such arbitrary criteria to the level of species, whose recognition in our view should continue to make reference to formational processes that have sundered groups of organisms that formerly interbred.

Nonetheless, for the sake of argument, let us consider what the proposal by Hendry and colleagues might entail for current taxonomic practice at the species level. Suppose, for example, that an arbitrary level of genetic divergence for species-level recognition were set at a magnitude that would enable continued (traditional) recognition of the numerous cichlid species in Lake Victoria. These sympatric fishes (recently diverged and reproductively isolated primarily by prezygotic barriers) are extremely close genetically (Meyer et al. 1990), far less so than local "conspecific" populations in many other vertebrate species [see, for example, pp. 321–323 in Avise (2000)]. Thus, by this standard criterion of genetic divergence, most currently recognized vertebrate species would then demand taxonomic subdivision into dozens if not hundreds of new "species". What useful purpose would this serve?

To counteract this problem, some higher genetic threshold for species recognition might be advocated that would alleviate this absurdity of excessive splitting. But any such arbitrary standard then by definition would exclude from formal recognition the Lake Victoria cichlids, for example. This too would be undesirable in our view because that artificial taxonomy would give no hint that something biologically interesting has occurred in the history of these fishes (or in any other organismal group where reproductive isolation was associated with less genetic divergence than the threshold arbitrarily adopted). Thus, old-fashioned though it may seem, we favor the retention of more traditional species concepts that retain a reference to biological processes. Although sometimes difficult to implement cleanly in terms of dichotomous nomenclature, these process-oriented species concepts nonetheless serve biology well by reflecting and also stimulating illuminating research into organismal ecology, behavior, conservation, and evolution.

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